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INFANTICIDE AND CANNIBALISM IN CHIMPANZEES, with Special Reference to the Newly Observed Case in the Mahale Mountains

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1. INTRODUCTION

While tracing the chimpanzees of M-group in the Mahale Mountains, western Tanzania, we had an opportunity to observe a cannibalistic episode on June 14, 1979.

Since Suzuki (1971, 1975) observed the first case of cannibalism among chimpanzees in the Budongo Forest, Uganda, in November 1967, 7 cases of infanticide and cannibalism were reported from the Gombe National Park, Tanzania (Bygott, 1972; Goodall, 1977) and 3 cases from the Mahale Mountains (Norikoshi, 1978; Nishida et al., 1979), and our case was the twelfth.

Infanticide and cannibalism in chimpanzees have been observed only 12 times in a twenty-year history of field studies since 1960 when these studies began at several localities in Africa. They can be said to be infrequent incidents in their society. However, the fact that they were seen at 3 localities being located far from each other reveals that they are by no means aberrant phenomena.

In this paper, I will first describe our observations, and will present the personal history of the victim's mother that can be traced in detail. This will be followed by the examination of blood relations between the victim and the captor, and of the social relations between the victim's mother and the captor. In the papers published so far, a few remarks have been made, such as: the victim's mother was a 'stranger' to the captors; both belonged to the same unit-group (Goodall, 1977); and she was an immigrant from a neighboring unit-group (Norikoshi, 1978). However, their further personal histories have not been mentioned.

The victim's mother in our case has been known over the years. She transferred from K- to the neighboring M-group, to which the captor belonged, and became pregnant therein. But only a few points in her personal history can be at present considered to have a connection with cannibalism.

However, one of the conspicuous features of chimpanzee society is that females 'voluntarily' transfer between unit-groups (Nishida & Kawanaka, 1972). Then, it may be one of the methods to make clear the sociological significance of cannibalism occurring in such a society that we present the social relations among the captor, the victim, and its mother in as much detail as possible.

The third, the characteristics of our case will be compared with those of the other cases. Because of insufficient data and the big differences of elements observed among cases, it might be impossible to draw a clear conclusion in all points through this comparison, but I would like to try to find out general features of infanticide and cannibalism seen in chimpanzees, and to discuss them from the sociological, ecological and ethological points of view, by comparing them with those in the other species.

Our cannibalistic episode was observed by Mohamedi Seifu of Kasoje Chimpanzee Research Station (KCRS) and me. The other data on chimpanzees in the Mahale Mountains

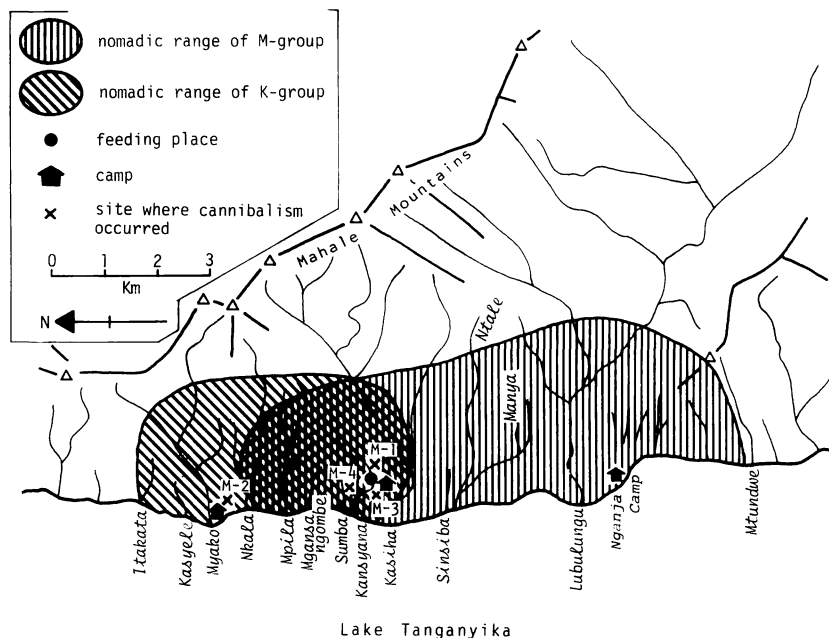


Fig. 1. Map of the study area and nomadic ranges of K- and M-groups, and the sites where cannibalistic episodes were observed.

which will be mentioned later in this paper have been accumulated by the research staff of KCRS in the course of researches which have been made since 1965. I worked at KCRS for a total 26 months between August 1969 and February 1970, between September 1972 and February 1973, and between June 1978 and July 1979, and mainly traced M-group. Habitat in our study area, methods of study, and the outline of the chimpanzees observed were described elsewhere (Nishida, 1968, 1979; Nishida & Kawanaka, 1972; Kawanaka & Nishida, 1975; Nishida et al., 1979: Fig. 1).

The social unit of chimpanzees (unit-group, Nishida, 1968; community, Goodall, 1971; etc.) will be called 'unit-group' in this paper as well, following the definition by Nishida & Kawanaka (1972) and Nishida (1979).

Age class and sex of chimpanzees will be hereafter abbreviated as follows: adult to A, young adult to YA, juvenile to J, infant to I, male to M, female to F, and estrous female to FE, which will follow Nishida's (1977) classification. AFE, for example, indicates an adult female in estrus. The cases will be abbreviated as shown in Tables 3, 5 and 6.

2. CANNIBALISTIC EPISODE

(1) Observation on the previous day (on June 13, 1979)

Prior to describing our observation of the cannibalistic episode, I would like to mention what we saw on the day before the incident. In June 1979, *Harungana madagascariensis* which was growing in the secondary forest covering a gentle slope along the eastern shore of the Lake Tanganyika bore fruit in abundance. The chimpanzees of M-group were feeding on the fruit, while moving mainly between the Sumba and Sinsiba Valleys.

On June 13 at 09:18 near K1 (see Fig. 2), we came across the members of M-group, Kajugi

(AM), Kalunde (AM), Fatuma (AFE), Ndilo (AFE), Wakampompo (AF) with Wamtumpa (IF), and Aji (JM; an orphan), who had come to the north across the Kasiha Valley. They slowly moved through K1 toward J1 while feeding mainly on the fruit of *Harungana* and additionally on the leaves of *Smilax kraussiana* and *Pteridium aquilinum*, the stalks of *Pennisetum purpureum*, and ants.

At 12:10 when we arrived at J1, Kajugi and Aji were eating the stalks of *Pennisetum*, but the others were not seen. At 13:05 low grunts of chimpanzees were heard from the bush north of J1, by which we knew the others to be resting there. After leaving J1 for a while, Kajugi returned there with Bakali (AM). They ate the pith of bananas and at 14:45 entered the northern bush to disappear.

At 14:55 Wakasunga (AF) and her son Lulemyo (JM) came up to J1 through the trail from the east. In their way they repeatedly glanced at the bush north of J1 where the others were resting. When the two intended to pass by us westward, we noticed a newborn infant being carried on her belly, and in order to look at it well we gave them sugar canes. They picked up the sugar canes and began to eat them on the trail about 5 m away from us.

Although this was the first time that I saw Wakasunga's newborn infant, it had already been found by Jumanne Katensi, a staff-member of KCRS, on May 2, when she was in company with chimpanzees of K-group. On both May 3 and May 29 she was observed in K-group, then she drew near M-group being accompanied by her newborn infant and Lulemyo.

At 14:56 just after Wakasunga began to eat some sugar cane, low grunts were emitted in the nearby bush at J1, and in no time she and Lulemyo went westward carrying the sugar cane and disappeared. We could not determine the infant's sex, but we found its face not to be so reddish and its eyes open.

Lubulungu (AM) appeared at the trail near J1 at 15:45 for the first time on this day, but soon returned into the bush. The chimpanzees that were resting in the bush gradually went northward and stopped for the night near the Sumba Valley.

(2) Observation of the cannibalistic episode

The chimpanzees of M-group that spent the night near the Sumba Valley repeatedly cried out there from the early morning on June 14. On our way to the middle stream of the Sumba Valley to continue our observation of them, we met Ntologi (AM) and Wamkime (AF) with her daughter Lusia (IF) at J1 at 09:30 and observed them till 10:10 (Fig. 3).

At 11:04 we came across Fatuma and Wakampompo at the site A (see Fig. 2) about 100 m

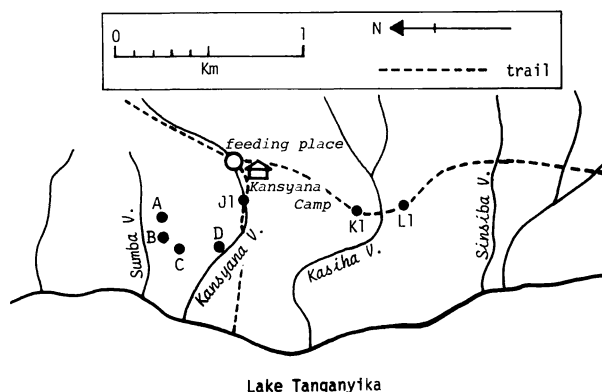


Fig. 2. Map showing the sites relating to the cannibalistic episode in June 1979 in Mahale.

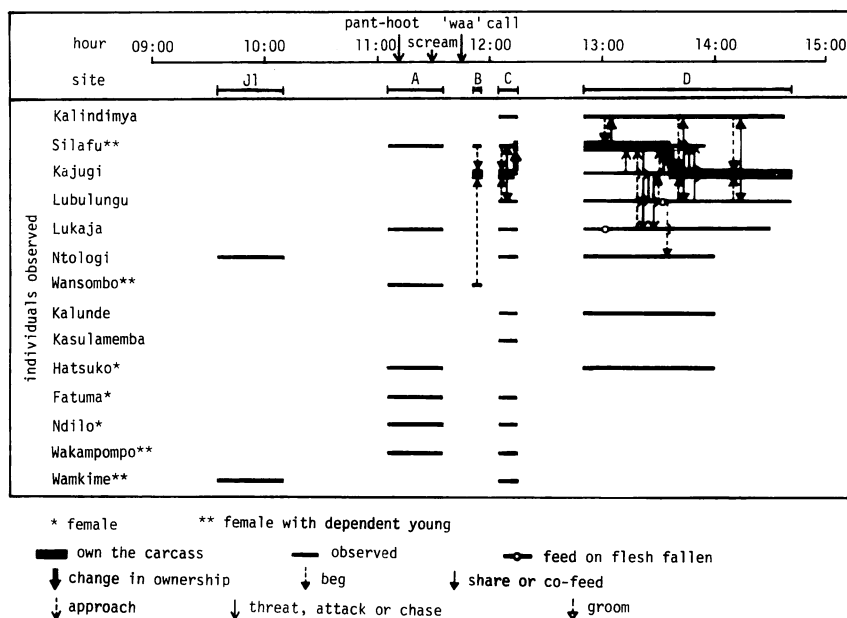


Fig. 3. Participants in the cannibalistic episode in June 1979, interactions among them, and change in ownership of the carcass.

south of the Sumba Valley. On the nearby tree of *Harungana*, Ndilo, Wansombo (AF) with her infant and Tende (JM), Silafu (AF) with Ryo (IM), Hatsuko (AFE), Lukaja (YAM) and Aji were eating its fruit.

At 11:13 at the site B about 100 m west of the site A pant-hoots were emitted by an adult male, who seemed to be Kajugi judging from the nature of the voices. At 11:30 an adult female screamed near the site B, and as if responding to it, Aji emitted low voice at the site A. Those who had been eating the fruit of *Harungana* at the site A climbed down the tree and went away toward the site B. On our way to trace them, we heard violent and loud 'waa' calls by an adult male from the site B, which were immediately followed by the same calls emitted near the site and at several places between the site and the Kansyana Valley.

Arriving near the site B at 11:50, we found Kajugi, Silafu, Wansombo and another female sitting side by side on a branch of a big tree of *Annona senegalensis*. Kajugi had a small blackish game in his right hand, to which the females were extending their arms. It was found out by binoculars to be a baby chimpanzee that Kajugi was holding. Soon afterwards, Kajugi climbed down the tree and rushed away southwest through the bush. The females followed him quickly and some others that were not seen also followed them emitting loud calls. We saw a blood-stain on the ground under the tree of *Annona*.

At 12:03 we caught up with Kajugi who was sitting under a shrub at the site C about 100 m southwest of the site B. He was holding a male infant which had not long been born and which was wounded in the face and seemed to be dead (Photo. 1). Kajugi was also wounded in the second finger of his left hand. Surrounding him, Kasulamemba (YAM), Lukaja and Aji were seen on the ground, and Ndilo and Ntologi on a tree. Although they all were habituated well to us, none of them drew near Kajugi who was sitting about 3 m away from us. Kalindimya (AM) approached Kajugi but went away without stopping. He seemed to be afraid of us



Photo. 1. Kajugi holding the carcass under the bush at the site C.



Photo. 2. Kajugi (left) biting the carcass and Lubulungu (right) looking at him.

crouching nearby since he was scarcely habituated. Lubulungu then came up through the bush and sat down close by Kajugi.

Kajugi tried to tear the carcass pulling its legs to both sides by using his mouth, hands and feet but could only slightly rip its left inguinal region (Photo. 2). He only bit off the tip of the toe and picked up a withered leaf of *Aframomum* to eat with the flesh, while holding the carcass in his left foot. In the meantime, Lubulungu drew the carcass toward himself to bite off a piece of flesh from its thigh (Photo. 3), with which he also ate a withered leaf of nearby *Aframomum*. Kajugi did neither reject Lubulungu at all nor loose his hold of the carcass.

At 12:05 Silafu carrying Ryo on her belly approached Kajugi from behind and reached her



Photo. 3. While Kajugi (left) picks up a withered leaf, Lubulungu (right) nibbles a piece of flesh.



Photo. 4. Silafu (center) pulls and bites the carcass which Kajugi is holding in his left foot.

arm over his shoulder to draw the carcass toward herself, but he pulled it back, so that she could not snap at it. Then, at 12:10, she drew it underneath his arm to nibble a piece of flesh. Neither Kajugi nor Lubulungu reproached her at all (Photo. 4).

At 12:14 Silafu again attempted to draw the carcass near her from Kajugi and this time he released it. Grabbing it from him, she rushed away to the southwest through the bush. Lubulungu and the others followed her immediately emitting 'waa' calls. Kajugi remained on the spot alone and lay on the ground for a short while. He soon rose up, pounded the ground with his hands emitting pant-hoots and then rushed away in the direction that Silafu and the others had taken. Fatuma approached him giving cries as if standing in his way, but he kept on going without taking any notice of her. At this time near the site C all other individuals except these two and two more, Ndilo and Wamkime, were not seen; they seemed to have already gone away following Silafu. In the vicinity of the Kansyana Valley about 300 m south of the site C, many chimpanzees repeatedly cried in chorus; Silafu and others seemed to be there (the site D).

When we arrived at the site D at 12:50, Silafu, embracing Ryo on her belly, was eating the carcass while seated on a big tree of *Pseudospondias microcarpa* standing on the right bank of the Kansyana Valley. On this tree, Kalindimya, Kajugi, Ntologi, Lubulungu, Kalunde and Hatsuko were seen, and Lukaja was under the tree. Of those in the tree only Kalindimya was close to Silafu and was extending his arm to her as if begging her for flesh, while the others were on the other branches surrounding the two at a distance and calmly looking at them.

Silafu turned her back on Kalindimya or made grimace at him, but she neither gave him a part of the carcass nor allowed him to touch it (Photo. 5). In the meantime, holding the carcass upside down by its legs, she little by little nibbled pieces of flesh from its abdomen, together with which she also ate leaves of the nearby *Saba florida*. The skin of the carcass's head had been already peeled off and the bone of its parietal part was exposed.

At 13:04 Kalindimya drew near Silafu again and stretched out his arm to her. She screamed making a grimace and dropped a piece of flesh from her mouth, which Lukaja picked up and gnawed under the tree. Silafu then peeled off the bone of the carcass's head to hand it to



Photo. 5. Kalindimya (right) approaches Silafu who is feeding on the carcass in a tree at the site D.

Kalindimya, and moved to the upper branch while he was gnawing it. After finishing the bone, Kalindimya approached again to Silafu and teased her for flesh, but she moved away little by little as if avoiding him without giving him anything more. At 13:13 Kajugi approached her but came down from the tree without teasing her like Kalindimya.

At 13:20 when Silafu moved from vine to vine of *Saba* carrying the carcass being followed by Kalindimya, Lukaja tried to approach her. She screamed and threatened him by swinging her arm, and he parted from her. Looking at this from a distance, Kajugi rushed at the tree and began a violent display shaking branches and vines, so that the others who were on the tree receded avoiding him. He then turned round and rushed at Lukaja and Lubulungu, who ran away at full speed. Kajugi then sat down on the ground and Lubulungu came up and groomed Kajugi for a short while as if coaxing him.

Kalindimya, who receded as well as the others while Kajugi was making his violent display, approached Silafu again after Kajugi stopped. At 13:32, Kajugi approached the two, and Silafu moved away a little to avoid him. He soon left her. When moving, Silafu dropped a piece of the carcass's viscera (probably intestine) on the ground, which Lubulungu picked up to eat together with a withered leaf of *Annona*. He then climbed up the tree of *Pseudospondias* and began to mutually groom with Ntologi.

At 13:39 Kajugi suddenly rushed at and raided Silafu, who screamed holding the carcass in her mouth and tried to elude him from vine to vine of *Saba*, but she was caught by him and let fall the carcass when she loudly screamed. Kajugi immediately jumped down to seize it, and after pounding it on the ground he climbed up the tree of *Myrianthus holstii* adjacent to the *Pseudospondias* tree. Kalindimya and Lubulungu climbed up the same tree and sat down on both sides of Kajugi.

These three immediately began to eat the carcass; every time they bit off a piece of flesh, they picked up flesh or withered leaves of *Uvaria angolensis*, *Myrianthus* or *Saba*. When Silafu intended to approach them at 13:45, Lubulungu and Kajugi shook their arms to threaten her, and she screamed and receded.

Although Kajugi never rejected the other two nibbling at the carcass which he kept holding, he never released it nor handed them a part of it which he tore off. While they were eating, other individuals who were surrounding them at a distance gradually left the scene and disappeared to the south, and at 14:03 only Lukaja remained under the tree. Kalindimya and Lubulungu sometimes threatened him emitting aggressive sounds and shaking vines and branches, but he did not recede.

At 14:38 when the carcass had been almost consumed, only a piece of skin being left, Kalindimya climbed down from the tree and went away southward; by this time Lukaja had disappeared. Kajugi then put all the remaining skin into his mouth at 14:41 and, after emitting pant-hoots on the branch, climbed down the tree to rush away to the south; Lubulungu followed him. The others had already gone away southward and the last two seemed to run after them.

At 18:02 on the day we observed the cannibalistic episode, Wakasunga made her appearance at the feeding place of the Kansyana Camp in company with Lulemyo, but she was not carrying her newborn infant that we had seen on the previous day. Neither she nor her son were wounded. They stayed at the feeding place till 18:20 eating sugar cane, then disappeared to the upper stream of the Kansyana Valley.

No females in either M- nor K-group except for Wakasunga lost their infants around the days the above incident happened, so that we can say it was Wakasunga's newborn infant that was killed and eaten by Kajugi and others.

3. WAKASUNGA'S PERSONAL HISTORY

(1) From 1966 to May 1978

Wakasunga was identified and named as a member of K-group in 1966, and was presumed to have been born around 1954 (about 12 years old at that time) on the basis of her physical characteristics (Nishida, 1968). She did not seem to have had a baby by that time, though she had already reached the age of sexual maturity.

She had her first infant, a male, in K-group around June or July 1967. The infant was seen to be alive till August 1968, but was missing in March 1969 when the field work was resumed (Nishida & Kawanaka, 1972). In April 1970 she had a second male infant, that also died probably on a tumor in its left leg in July 1971, and she was seen carrying its dead body (Nishida, 1973). Toward May to June 1973 she gave birth to her third infant that was also a male and was named Lulemyo (Kawanaka & Nishida, 1975), which has been brought up in safety.

She remained in K-group even after giving birth to Lulemyo and five years after the delivery, toward the end of April 1977, she again showed signs of estrus, though that time she was not seen to copulate. At the end of September, after five months, she became estrous again and was copulated with by males of K-group (Uehara, unpublished). She remained in this group for about the subsequent six months.

(2) From May 1978 to June 14, 1979

Wakasunga had always belonged to K-group for more than 12 years, but she was found, for the first time, moving together with chimpanzees of M-group on May 20, 1978, by Alimasi Kasulamemba (Figs. 4 & 5). This time she was not estrous and was not accompanied by Lulemyo. While she was in K-group, she was always carrying Lulemyo but this time he remained in K-group alone (Uehara, unpublished).

Between May and October in 1978, she always moved with the members of M-group, and was observed relatively frequently (Fig. 6). Besides, irrespective of her sexual condition, she

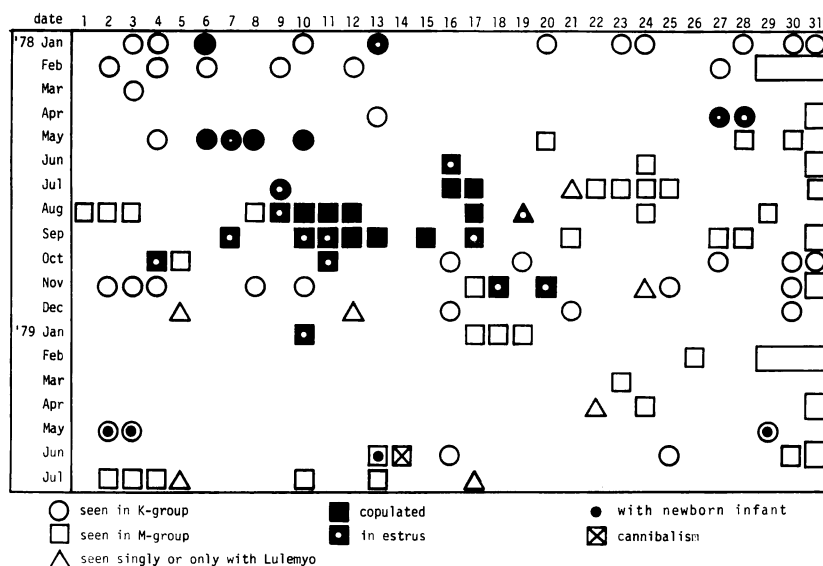


Fig. 4. Records of observation of Wakasunga between January 1978 and July 1979. (Data on K-group between January and November, 1978, and those on M-group between January and May, 1978, are offered by Uehara [unpublished].)

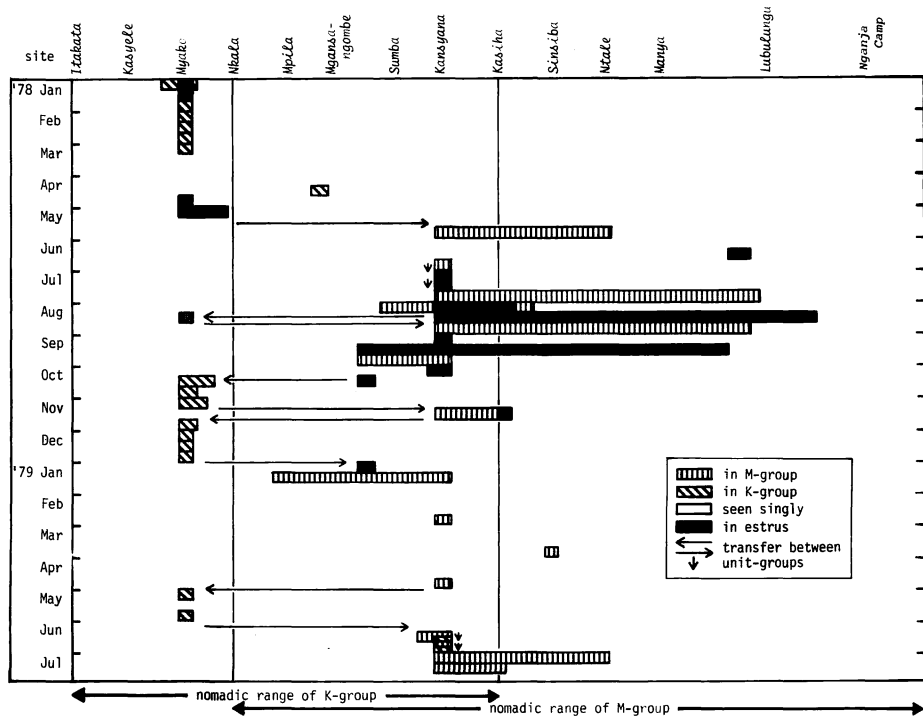


Fig. 5. Locality and unit-group in which Wakasunga was observed, and her sexual condition between January 1978 and July 1979. (Source of data is as Fig. 4.)

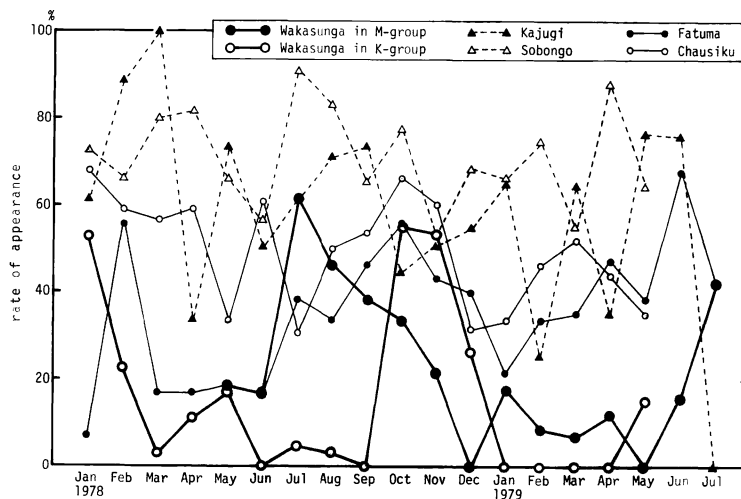


Fig. 6. Monthly distribution of rate of appearance of Wakasunga as compared with those of the individuals that were most frequently observed in each unit-group: in M-group, Kajugi (♂) and Fatuma (♀); in K-group, Sobongo (♂) and Chausiku (♀). (Source of data is as Fig. 4.)

$$\text{rate of appearance} = \frac{\text{no. of days when each individual was observed}}{\text{no. of days when each unit-group was observed}} \times 100$$

was seen to cross the southern boundary of the nomadic range of K-group to the south and to reach Nganja area which was located about 4 km south of that and which was at the southernmost part of the nomadic range of M-group (Fig. 5). She had never been seen at the outside of the nomadic range of K-group before May 1978.

During this period, she once moved in company with members of K-group and once made movements to give the strong impression that she did so. The former was seen on July 9, when she appeared at the feeding place of the Kanyana Camp with 13 chimpanzees of K-group including Sobongo (AM) and Kamemanfu (AM). The latter was seen in August. On August 17, she was found at Nganja in the daytime with many individuals of M-group, while at 19:00 she alone reached at the Kanyana Camp about 4.5 km north of Nganja as the crow flies. Two days later, on August 19, she appeared, also alone, at the Myako Camp. Then, on August 24, she was again found with many chimpanzees of M-group at the right bank of the Lubulungu Valley near the southern boundary of nomadic range of M-group (Fig. 5).

At this time she was accompanied by Lulemyo whom she had left in K-group since May. During the six days between the 19th and 24th she was not seen with the members of K-group, but that she rejoined M-group in company with Lulemyo showed that she had some connections with those of K-group during this period. From then onwards this pair of mother and son has always been seen together.

After rejoining M-group bringing Lulemyo, Wakasunga became estrous both in September and at the beginning of October, and she was seen, especially at the middle of September, to be copulated with by males of M-group (Table 1, Figs. 4 & 5, Photo. 6). While she was in M-group, she also conducted begging behavior toward males (Photo. 7). When Kajugi hunted a bushbuck fawn in August 1978, for example, she was given a part of its skin (Kawanaka &

Table 1. Adult and young adult males who were observed to copulate with Wakasunga in 1978. (Data between January and May are offered by Uehara [unpublished].)

	date													
name	Jan. 6	May 6	8	10	July 16	17	Aug. 10	11	12	17	Sep. 12	13	15	
K-group														
Kasonta*	○													
Kamemanfu	○													
Sobongo		○		○	○									
Masisa														
M-group														
Kalindimya														
Mimikire								○	○				○	
Kagimimi					○ ¹			○	○					
Rashidi														
Kajugi					○	○	○				○		○	
Ntologi														
Bakali						○		○				○		
Nishida**														
Lubulungu								○	○	○	○			
Musa					○									
Kalunde														
Lukaja					○						○ ¹			
Kasulamemba													○ ²	

*: disappeared at the end of January 1978 (Uehara, unpublished).

** : disappeared at the end of April 1978 (Uehara, unpublished)

¹: observed to copulate twice a day.

²: observed to copulate three times a day.



Photo. 6. Wakasunga being copulated with by an adult male of M-group, Bakali, and Lulemyo approaching them.



Photo. 7. Wakasunga (right) is begging Kajugi (center) for banana. Kagimimi (left) is slightly threatening her.

Mohamadi Seifu, unpublished). Thus, she had a very normal relation with both males and females of M-group and never showed unusual behavior. This agrees with the behavior of other females who had transferred so far (Nishida & Kawanaka, 1972).

After the middle of October 1978, however, she and Lulemyo seldom moved with the members of M-group. Instead they were often seen to move with those of K-group (Uehara, unpublished), which lasted till the end of 1978. During this period except that she was once seen with members of M-group at the southern part of the nomadic range of K-group, she was

Table 2. Chimpanzees of K-group who were seen together with Wakasunga in May 1979. (From the field notes of Jumanne Katensi and others. Only adults and young adults are listed.)

name	date		
	May 2	May 3	May 29
males			
Kamemanfu	○	○	
Sobongo	○	○	
Masisa	○	○	
females			
Wabunengwa	○	○	
Chausiku*	○	○	○
Wangala*	○	○	
Wantangwa			
Wamikambi*			
Wasalamba			
Wangulu			
Wabwema*			
Wakiluhya*	○		
Wantendele*	○	○	
Gwekulo			○
Wakapala			
Gwamami	○	○	

*: females with dependent young.

seen at the vicinity of the Myako Valley lying to the north of the northern boundary of that of M-group, and yet she was frequently seen (Fig. 6). It may be said, therefore, that she could be reckoned as a member of K-group from both viewpoints of her range of movement and of her social relationships with the others. But it was only when she was seen with those of M-group at the middle of November that she showed signs of estrus during this period.

From the beginning of 1979 she again left the vicinity of the Myako Valley to be seen at the area between the Mpila and Sinsiba Valleys which was utilized mainly by M-group in those days, as if she had broken with K-group, though she was observed only a few times. This lasted until April 24 when she, this time accompanied by Lulemyo, appeared at the Kansyana Camp together with Kagimimi (AM) of M-group.

She, however, returned northward again and made her appearance together with the many individuals of K-group at the vicinity of the Myako Valley on May 2 (Table 2), and she was confirmed, for the first time, to carry her newborn infant by Jumanne Katensi, as mentioned already. It is considered between April 24 and May 2 that she gave birth to her fourth infant, and just before or after the delivery she joined K-group. She and her two children were also seen in K-group on May 3 and 29. Jumanne Katensi informed me that she groomed with the others but did not show any unusual behavior toward them. After May 29 she did not make her appearance for about a half month until June 13, the day previous to the incident of cannibalism.

(3) After June 15, 1979

At one-day's interval after Wakasunga and Lulemyo went away to the upper stream of the Kansyana Valley in the evening on June 14, they appeared at the feeding place of the Kansyana Camp in company with Wasalamba (AM), Wabunengwa (AF) and Wakapala (AF) of K-group, and again on June 25 together with Wasalamba, Wabunengwa and Wabwema (AF) with Kahaso (IM). Thus, Wakasunga was accompanied by females of K-group after cannibalism, but was never observed to move with males of this group.

She and Lulemyo joined M-group toward June 30 and began to move southward crossing

the southern boundary of the nomadic range of K-group. On September 1, about 2.5 months after her infant was killed, she became estrous in M-group (Nishida, Takahata & Mohamedi Seifu, unpublished).

4. NOTES ON INFANTICIDE AND CANNIBALISM

(1) Age and sex of the victims

Wakasunga's infant was born between April 24 and May 2, 1979, and was killed on June 14, 1.5 months after his birth. The victims' ages in the 12 cases including our case cover a relatively wide range from newborn still having umbilical cord (B-1; see Table 3) to 3 years old (M-1). They all, however, fell under the infant stage in classification by Nishida (1977), that is, all of them were those being carried by their mothers while traveling, but no juvenile that could travel by himself has been seen to fall a victim to cannibalism.

In the cases from Gombe that females harmed infants (G-2, -5, -6, -7), all the victims were newborn infants of 1 to 3 weeks old, by contrast with which those of the cases in which males were the captors covered a wider age range.

All the victims of the 4 cases in Mahale were males, while in Gombe, both male and female victims were seen in 3 cases, respectively, and sex unknown in one case. In category (a) classified by Goodall (1977), that is, in cases where infants of 'stranger' females were killed by adult males of the Kasakela community (G-1, -3, -4), the victims of a male, of a female and of sex-unknown were seen in one case each. In category (b), that is, in cases that infants

Table 3. Comparative data on infanticide and cannibalism in chimpanzees - (1).

abbrev.	case		victim's age/sex	relation between captor and victim's		sources
	locality	date		mother	father ²	
B-1	Budongo	Nov. 67	newborn/?	?	?	Suzuki, 1971
G-1	Gombe	Sep. 71	1.5-2 yrs/?	stranger	other	Bygott, 1972, Goodall, 1977
G-2	Gombe	Aug. 75	3 weeks/♀	same (♀) ¹	same	Goodall, 1977
G-3	Gombe	Oct. 75	1.5-2 yrs/♂	stranger	other	Goodall, 1977
G-4	Gombe	Nov. 75	1.5-2 yrs/♀	stranger	other	Goodall, 1977
G-5	Gombe	Jan. 76	1 week/♂	same (♀)	same	Goodall, 1977
G-6	Gombe	Oct. 76	3 weeks/♂	same (♀)	same	Goodall, 1977
G-7	Gombe	Nov. 76	3 weeks/♀	same (♀)	same	Goodall, 1977
M-1	Mahale	Apr. 74	3 yrs/♂	other	other	Nishida et al., 1979
M-2	Mahale	Jan. 76	1.5 yrs/♂	other	other	Nishida et al., 1979
M-3	Mahale	Jan. 77	2 months/♂	immigrant	same	Norikoshi, 1978
M-4	Mahale	Jun. 79	1.5 months/♂	immigrant	same	(this study)

¹: (♀) indicates that the captors were females.

²: victim's biological father; 'other' indicates that the father belongs to a unit-group other than that of the captor, and 'same' that both belong to the same unit-group.

Table 4. Combination of victims' sexes with those of captors or cannibals in the cases of infanticide and cannibalism in chimpanzees.

	captor/cannibal		total
	♂	♀	
victim			
♂	5	2	7
♀	1	2	3
?	2	0	2
total	8	4	12

within the Kasakela community were killed by females of the same community (G-2, -5, -6, -7), both male and female infants were killed twice, respectively. Thus, no correlation was seen between the victim's sex and the categories in Gombe.

Considering the cases as a whole, however, in the 12 cases 7 were males, 3 were females and the victim's sex of the remaining 2 was unknown (Table 4). If we take up only the cases where the captors or cannibals were males, that is, all the cases except for those in category (b) in Gombe, victims of males were seen in 5 cases, while females only in 1 case and sex-unknown in 2 cases. It seems, therefore, that more male infants were killed by conspecifics than female infants, and this trend was more apparent in the cases where the captors were males.

(2) Relations between the victim's mother and the captor

The victim's mother in B-1 was not known (Table 3). All the captors of 7 cases in Gombe were members of the Kasakela community or were thought to be so (Goodall, 1977). In 3 cases, (a) the victims' mothers were 'strangers' and the captors were adult males of the Kasakela community (G-1, -3, -4), while in the other 4 cases, (b) both mothers and captors were adult females of this community (G-2, -5, -6, -7). The victims' mothers in category (b), Gilka and Melissa, lost their 2 infants, respectively, by cannibalism (Goodall, 1977). Gilka is Olly's daughter and was born in the Kasakela community (Goodall, 1975). Melissa is supposed to be a sister of the two males of this community, McGregor and Humphrey (Goodall, 1975), and there is a strong presumption that she was born in this community. In category (b), therefore, the victims were infants to which their mothers gave birth in their own native unit-group (or very probably so). Passion, the captor in this category, had already reached the age of full adult before she was named (Goodall, 1975), but her native unit-group was unknown.

None of the 'stranger' females of category (a) joined the Kasakela community after their infants were killed, nor mothers in category (b) left this community.

The 4 cases in Mahale cannot be classified as simply as those in Gombe. This is due to their social structure that almost all females transfer at the time when they reach the age of sexual maturity.

The victim's mother in M-1 Wamkime belonged to M-group when the incident occurred, but her baby was killed and eaten by adult males of K-group (Nishida et al., 1979). However, she was observed in K-group in May and in September, 1967, and in September 1968 she was found in M-group (Nishida, 1968; Nishida & Kawanaka, 1972). Although her personal history after the transfer can not be completely traced, it is thought that she has belonged to M-group ever since September 1968 because, whenever she was observed, she was in company with the members of M-group. She gave no evidence of joining K-group after cannibalism, but kept on staying in M-group to have a baby in 1975 (Uehara & Norikoshi, unpublished).

Wantendele, the victim's mother in M-2, joined K-group from the outside around August 1972 (Kawanaka & Nishida, 1975). She had never been observed before that time, so that from where she came is unknown. 2 years after joining K-group, she had an infant, that she lost by cannibalism, and then she remained in K-group to have a male infant Masudi in 1977 (Nishida, unpublished). Masudi has been safely brought up and belongs to K-group together with his mother.

Ndilo, the victim's mother in M-3, has been known ever since 1966 when members of K-group were identified, and in those days she was always in company with her mother Wantangwa (Nishida, 1968). Ndilo was thought to be born in K-group around 1963. Although her close proximity to her mother lasted until 1970 (at the age of 8), it markedly lessened in 1971 and she eventually transferred to M-group toward September of that year (Nishida, 1979). She has belonged to M-group ever since, though she returned to K-group three times, between December 1971 and July 1972, in February 1973 (Kawanaka & Nishida, 1975; Nishida, 1979), and in February 1974 (Uehara, unpublished).

She had her first infant in M-group in May 1975, which died in the following month (Nishida, unpublished). In November 1976, she had her second male infant named Humbe, which was killed and eaten in January 1977 by Kagimimi and other males of M-group (Norikoshi, 1978). Even after cannibalism she kept on staying in M-group, where she gave birth to her third infant, which was a female named Semeni, at the end of 1977 to the beginning of 1978 (Uehara, unpublished), who disappeared in March 1979. Since nobody saw Ndilo carrying her baby's dead body, it might be possible to think that Semeni also fell a victim to cannibalism if we take the way of thinking by Goodall (1977). However, in those days we did not obtain any objective evidence suggesting this such as feces containing hair of chimpanzees, so I will not examine Semeni's disappearance further.

As mentioned above, Ndilo was by no means a 'stranger' to the captors, so that this case does not fall under either category (a) or (b) classified by Goodall (1977) as was pointed out by Norikoshi (1978), nor did she leave M-group after the incident.

Relations between the last victim's mother Wakasunga and the captor were the most complicated. She was never a 'stranger' to the captor, so this case, too, is not covered by Goodall's categories. Although she became pregnant after having sexual relations with males of M-group, she was in K-group between the time just before or after delivery and the time before the incident. Such movements of the victim's mother was recorded for the first time. While she did not show any unusual behavior in K-group, she seemed to be strained when she approached M-group judging from her countenance and deportment. This was probably not caused by our presence because they sat down close by us when eating sugar cane, nor was it thought to be due to a predator like a leopard because the chimpanzees of M-group were calmly resting. It was, therefore, very plausible that Wakasunga took precautions against chimpanzees of M-group and was strained because of them.

Wakasunga behaved as usual when she was both in K- and in M-groups before delivery, while after that she took a different attitude toward each unit-group. Although it is hard to speculate further on this difference, one cause might be that after delivery she had relations first with members of K-group and then approached M-group. If so, it seems that she alone was aware of this and was strained. It is much harder to understand why she dared to approach M-group against which she had to take precautions.

She was in company with the members of K-group temporarily before and after cannibalism, and then she rejoined M-group, in which she began to show signs of estrus. It might be said that she was the only female who was integrated into the captor's unit-group after the incident.

Goodall (1977) classified the cases of infanticide and cannibalism in chimpanzees of Gombe into two categories, but it is clear that all the cases do not necessarily fall under either category. Nor can it be always affirmed that "cannibalism may basically be an inter-unit-group phenomenon" (Nishida et al., 1979, p. 18).

Norikoshi & Kitahara (1979) say that there are 4 possible combinations between the captors and the victims of cannibalism in chimpanzees: (1) males kill and eat an infant of a neighboring unit-group (or of a stranger female), (2) males eat an infant of their own unit-group, (3) females eat an infant of their own unit-group, and (4) females eat an infant of a neighboring unit-group, and that the cases of (1), (2) and (3) have been seen so far. Taking personal histories of the victims' mothers into consideration, however, the combinations cannot be so simply classified. The most problematic point in their argument is that they do not take into consideration the fact that every unit-group contains immigrant females.

The cases in which the captors or the cannibals were males occupied 8 of 12 cases and exceeded in number those in which they were females (Table 4). Besides, the former cases

were seen in all 3 localities of Budongo, Gombe and Mahale, while the latter cases were seen only in Gombe.

(3) Biological father of the victim

On the gestation period of chimpanzees several data have been offered so far: e.g. 196 to 260 days (Gavan, 1953), 225 days (Riopell, 1963), 202 to 261 days (Kingdon, 1971), 227 days on the average (Keeling & Roberts, 1972), and so on, by which it can be thought to last for a seven-to-eight-month period.

Wakasunga gave birth to her fourth infant between April 24 and May 2, 1979, so that it is plausible that she conceived it at the end of August to the beginning of October of 1978. In those days of her conception she was in M-group, where she became estrous and was copulated with by its males (Table 1, Figs. 4 & 5). In and after October 1978 she mostly moved together with the members of K-group but was not estrous.

From these facts, it is very probable that Wakasunga became pregnant in September 1978 and the infant's biological father was one of the males of M-group. Kajugi and the other cannibal males, therefore, killed and ate the offspring of the same sex which was related by blood to one of the males of their own unit-group.

Of the cases reported so far, nothing is known about this blood relation in B-1 (Table 3). In 3 of 7 cases in Gombe (G-1, -3, -4) of category (a), the victims' biological fathers and the captors belonged to different unit-groups from each other, while in the remaining 4 cases of category (b) (G-2, -5, -6, -7), both belonged to the same unit-group.

Judging from the records of the victims' mothers in Mahale before each incident happened, the biological fathers of the victims in M-1 and M-2 belonged to unit-groups other than the captor, while in M-3, as in M-4, both belonged to the same unit group.

On this point the cases in Mahale, too, can be classified into two, but these do not correspond with those set up on the cases in Gombe. In other words, adult males do not always kill infants carrying genes of those of the other unit-group.

Table 5. Comparative data on infanticide and cannibalism in chimpanzees - (2).

case	attack on mother*	process of consumption	consumers
B-1	?	<i>intermittently</i> eaten for more than 2 hrs, early and last stages of consumption were not seen.	♂ ♂
G-1	+	<i>intermittently</i> eaten for 6 hrs, a fairly large portion of the carcass was abandoned.	♂ ♂
G-2	+	<i>continuously</i> eaten for 5 hrs.	♀ ♀
G-3	?	a mere scrap of flesh was eaten, but a large portion was abandoned.	♂ ♂
G-4	+	(<i>not eaten</i> , but "rescued".)	—
G-5	?	(killed but <i>not eaten</i> , the mother was seen carrying dead infant.)	—
G-6	+	<i>continuously</i> eaten for 5 hrs.	♀ ♀
G-7	+	<i>continuously</i> eaten for more than 2 hrs, last stages of consumption were not seen.	♀ ♀
M-1	?	only the last stage of consumption was seen, <i>most of the carcass was consumed</i> .	(♂ ♂)
M-2	+(?)	(process of consumption was not seen.)	?
M-3	-(?)	<i>intermittently</i> eaten for more than 8 hrs, on the next day a male was seen carrying a piece of skin of the carcass.	♂ ♂
M-4	-(?)	<i>continuously</i> and almost <i>entirely</i> consumed within 3 hrs.	♂ ♂ ♀

*: attack on the victim's mother by the captor(s); + indicates that the mother was severely attacked, — that she was not or not so severely attacked, ? that the scene in which the victim was seized was not seen, and (?) that they were judged from the circumstantial evidences.

(4) Attack on the victim's mother by the captor

We could not observe the scene where the victim in M-4 was seized by the captor, but its mother did not seem to have been severely attacked by the captor, since neither she nor the victim's brother were wounded (Table 5): but she might have resisted the captor somewhat, since Kajugi was wounded in his finger.

Most of the participants in the scene where Wakasunga's infant was eaten had been seen at other sites before the outbreak of the incident and gathered after it (Fig. 3). Those who were found after its outbreak for the first time on that day were four males of Kalindimya, Lubulungu, Kalunde and Kasulamemba except for Kajugi. Although it cannot be denied that some of these four took part in seizing the infant, it may be more plausible to judge that Kajugi alone seized it for the following reasons: (a) pant-hoots were emitted by only one male, probably by Kajugi, (b) the scream by a female lasted only for a short while, (c) 'waa' calls were emitted by one male, and then were emitted in chorus around the place, (d) the females who were seen with Kajugi at the site B had already been seen at the site A, and (e) the above four adult males were not seen at the site B, but were observed later at the site C or D for the first time.

Ndilo in M-3 does not seem to have been hurt either according to the Norikoshi's description (1978), which implies that she would not have been attacked very severely, if at all. By contrast, Wantendele in M-2 was seriously wounded in her elbow and buttocks (Nishida et al., 1979). Judging from her injury, it seems that the captor severely attacked her and that she frantically resisted.

It is worth noting the difference that Wakasunga and Ndilo were not 'strangers' to the captors on one hand, and that Wantendele's infant seems to have been harmed by chimpanzees of the unit-group other than her own on the other. However, we have not obtained sufficient data to affirm whether this difference caused the captors to attack victim's mother or not. That Wakasunga and Ndilo were robbed of their babies without being severely attacked implies that infanticide in chimpanzees does not always result from aggression against the mothers.

As mentioned above, we noticed the difference among the cases in Mahale, by contrast with which in every case in Gombe cooperative attacks on the victim's mother by a gang of chimpanzees were seen whenever the incidents were observed from the beginning (Goodall, 1977).

All the cases in which captors were males seem to have happened unexpectedly both in Gombe and in Mahale, while in the cases of category (b) in Gombe the captors Passion and her daughters seem to have shown interest in the particular infants for some time before the incidents (see Fig. 1 in Goodall, 1977, p. 267). This difference might be due to the captors' sex.

Suzuki (1971, 1975) emphasizes that there may be a connection between meat-eating and cannibalism in chimpanzees on one hand and their excited state caused by changes of food seasons on the other. Nishida et al. (1979), however, pointed out that meat-eating in Mahale does not always agree with Suzuki's statement. M-4 broke out in the midst of the food season of *Harungana*, and we did not record any unusual excitement in chimpanzees of M-group in the course of tracing them for several successive days before the incident. They were very calmly feeding even just before its outbreak. So M-4, too, disagrees with Suzuki's statements.

(5) Process of consumption

The victim in M-4 was continuously and almost entirely consumed within 3 hours after being seized, though the process was interrupted for a short while when the owners changed (Table 5). In M-1 it was unknown how long it took the cannibals to consume the carcass, but it is said that "most of the carcass has already been consumed" (Nishida et al., 1979, p. 17). The cannibals in M-3 seized their victim in the morning on the day of the incident and continued to eat its carcass for more than 8 hours until the evening; besides, an adult male

was seen carrying a part of its skin even on the next day (Norikoshi, 1978). It is not described how much of the carcass was eaten, but judging from the small part of its skin left most of it may have been consumed.

In this case, Norikoshi (1978) emphasizes that the carcass was very slowly consumed and says, taking behavior of individuals surrounding the cannibals into account, that "it may be possible to be said that strong inhibition works upon cannibalism in chimpanzees" (p. 10). However, it should be said that the fact that the cannibals continued carrying and eating the carcass for such a long time without discarding implies that they were strongly attracted by its flesh.

The cases in Gombe seem to be somewhat different from those in Mahale also on this point. The carcasses in G-2, -5, and -7 of category (b) were continuously consumed for about 5 hours or for more than 2 hours (Goodall, 1977), which were similar to M-4. By contrast, the victim in G-1 was carried for over 6 hours, during which it was eaten intermittently and for only a few minutes at each time, but a large portion was eventually abandoned (Bygott, 1972; Goodall, 1977). Besides, it was said that the victim in G-4 was not eaten but was "rescued" (Goodall, 1977).

Thus, adult males in Gombe and in Mahale showed different behavior when they dealt with the victims. Yet the data obtained so far are insufficient to make clear the cause of this difference and its meanings. It is said that in cases of normal meat-eating in Gombe carcasses were almost entirely consumed (Bygott, 1972; Teleki, 1973), but that in cases in Mahale "a fairly large portion of the carcass is sometimes discarded without being consumed" (Nishida et al., 1979, p. 19), though a bushbuck fawn hunted in August 1978 in Mahale was almost entirely consumed. Even if this is taken into consideration, the clear difference seen between males in Gombe and those in Mahale is not explainable.

"Wadging" mentioned in cases of normal meat-eating (Teleki, 1973; Nishida et al., 1979) was observed in M-4 as well. I would like to point out here that 'withered leaves' were also eaten with flesh in M-4, since they were scarcely taken in the normal plant-eating of chimpanzees.*

(6) Change in ownership of the carcass

Kajugi was snatched the carcass by Silafu after he nibbled only a bit of its flesh (Fig. 3, Table 6), which made a sharp contrast with the case of normal meat-eating in August 1978 in which Kajugi continued to eat the carcass without releasing his hold till he allowed Waka-sunga to take away a remnant of a part of skin, 3 hours after the kill, though he did not refuse a few males to co-feed on it with him.

Change in ownership of carcass was also seen in M-3 (Norikoshi, 1978) and in most cases in Gombe (Bygott, 1972; Goodall, 1977). This may imply that this change is a common feature of cannibalism but is in contrast to normal meat-eating. It is not necessarily said, however, "this suggests that prey was less attractive as a food object, and more an object of curiosity than other animals" (Bygott, 1972, p. 411), but the meanings of this phenomenon are still unclear.

(7) Bizarre behavior

Goodall (1977, p. 279) says that "the adult males, both at Gombe and at Budongo, showed behavior which differs from that seen during normal meat-eating", and that they showed such "very abnormal patterns" as follows: "(a) repeatedly charging and flailing the body, (b) the poking at and examination of the body, (c) the pounding on the chest or head with fists,

*Withered leaf eating was also recorded when they hunted and ate a bushbuck fawn in August 1978 (Kawanaka & Mohamedi Seifu, unpublished).

Table 6. Comparative data on infanticide and cannibalism in chimpanzees - (3).

case	change in ownership	bizarre behavior
B-1	?	±**
G-1	+	+
G-2	+*	—
G-3	+	+
G-4	+	+
G-5	?	?
G-6	+*	—
G-7	+*	—
M-1	?	?
M-2	?	?
M-3	+	?
M-4	+	—

*: change occurred only among a mother and her daughters.

**: original observer (Suzuki, 1971, 1975) only mentioned 'playing'.

and (d) the playing with or grooming of the body"', and emphasizes that in this point her two categories are in sharp contrast to each other.

Such behavior, however, was never seen in M-4, nor was it mentioned in the report on M-3 (see Norikoshi, 1978), both of whose captors and cannibals were adult males (Table 6). Therefore, "bizarre behavior" described by Goodall (1977) is not always seen in every case where adult males were the cannibals.

Describing Kajugi's behavior in M-3 that he attacked the individuals who were eating the victim or other individuals who approached it, Norikoshi (1978, p. 11) says that "it is clear that this Kajugi's behavior resultingly worked as a social mechanism to inhibit cannibalism".

However, in M-4 it was none other than Kajugi who played a leading part. Although he did nothing to Kalindimya who approached and teased for flesh to Silafu who robbed Kajugi of the carcass, he attacked and chased Lukaja who tried to approach her; besides, he eventually raided her by himself to take back the carcass and entirely consumed it without any delay and without releasing it. It may be plausible to consider that in M-4 Kajugi intended to prevent his inferior from getting flesh and that he simply wanted to take possession of it.

(8) Sexual condition of females of the captors' unit-groups about the time when the incidents happened

This problem on which little attention has been paid so far will be examined on M-4 alone. In 1979 it was considered that adult females belonging to M-group amounted to about 40, of which 29 were identified (Table 7). 16 of the 29 females became estrous or were sexually

Table 7. Sexual conditions of adult females of M- and K-groups in the days around the occurrence of M-4.

	a no. of adult females	b sexually active	c sexually inactive	d no. of adult males	e b/d
M-group*	29+**	16+	13+	11	1.5+
K-group	13**	8(5)***	5	3	2.7(1.7)

*: about ten more females seem to belong to M-group but they are not recognized.

**: both include Wabunengwa who went to and fro between M- and K-groups. She was estrous and was copulated with in both unit-groups.

***: although 8 females had no infant and, so, ought to be sexually active, 3 of them did not show a sign of estrus.

*On B-1, Suzuki (1971, 1975) only mentions "playing".

active without an infant in May to June 1979 before the occurrence of M-4, but the remaining 13 were sexually inactive, because they had dependent young at an infant stage. The former females were 1.5 times as numerous as the 11 adult males of M-group.

At that time 13 adult females belonged to K-group, 5 of which were sexually inactive. Although the remaining 8 females had no infant, 3 of them who were very old had not shown signs of estrus for a considerably long time, but the other 5 were cycling. These were 2.7 or 1.7 times as many as the adult males of K-group.

The ratio of sexually active females to adult males in M-group was slightly smaller than that in K-group, while we have never seen that relations among adult males in M-group were strained scrambling for estrous females. Besides, Kajugi, the captor in M-4, was one of the most superior males in M-group and was almost always seen to be near estrous females and to copulate with them whenever they were (see Table 1). It cannot be thought, therefore, that he had a pent-up sexual desire by which he was driven to kill an infant.

It has been said that sexual relations in chimpanzees were generally promiscuous (Goodall, 1965; Nishida, 1968), while recently such cases have been known where a couple of a male and female formed a consort relationship and moved far away from the other members of their own unit-group (Goodall, 1968; Tutin, 1975; McGinnis, 1979; Nishida, 1979). In M-group, too, Ntologi and Wakakumo (AF) were sometimes to form such a relationship and to appear at Nganja far apart from the others in 1979. On June 5 and 7, 1979, a week before the occurrence of M-4, these two were seen at Nganja, but, as mentioned already, Ntologi made his appearance at the scene of M-4 without being accompanied by Wakakumo. It is unclear, however, whether such Ntologi's behavior as above had some effects upon the other adult males of M-group, particularly upon Kajugi, nor whether it had some connection with cannibalism or not.

5. SOME OTHER PROBLEMS CONCERNING INFANTICIDE AND CANNIBALISM

I would like to present and to examine the data from Mahale which will be necessary for discussing the background and significances of infanticide and cannibalism.

(1) Change in spatial relationships between M- and K-groups, and in population density in a limited area

M- and K-groups extensively overlap their nomadic ranges and at least till 1973 they migrated seasonally twice a year; both migrated northward in September to November, which was the end of the dry season, and southward in January to March, the end of the food season of *Saba florida*; M-group in the rainy and K-group in the dry seasons, respectively, monopolized the overlapping area (Nishida & Kawanaka, 1972; Nishida, 1979). Recently, however, M-group ceased to move away southward even after the food season of *Saba* was over, but began to utilize its whole nomadic range including the overlapping area throughout the year, while K-group ranged the overlapping area in the interval when members of M-group went away to the southern part of its nomadic range (Fig. 7).

Population size of K-group changed slightly during a long period (Nishida, 1979), and also that of M-group does not seem to have increased. Moreover, no unit-group has invaded Mahale from the surrounding area; so the overall population density in Mahale cannot be thought to become higher. It can be said, however, that the population size of chimpanzees that ranged the overlapping area throughout the year, and chances of encounters between the two unit-groups increased according to the change in spatial relationships between them.

All the 4 cases of cannibalism in Mahale occurred within or near the overlapping area

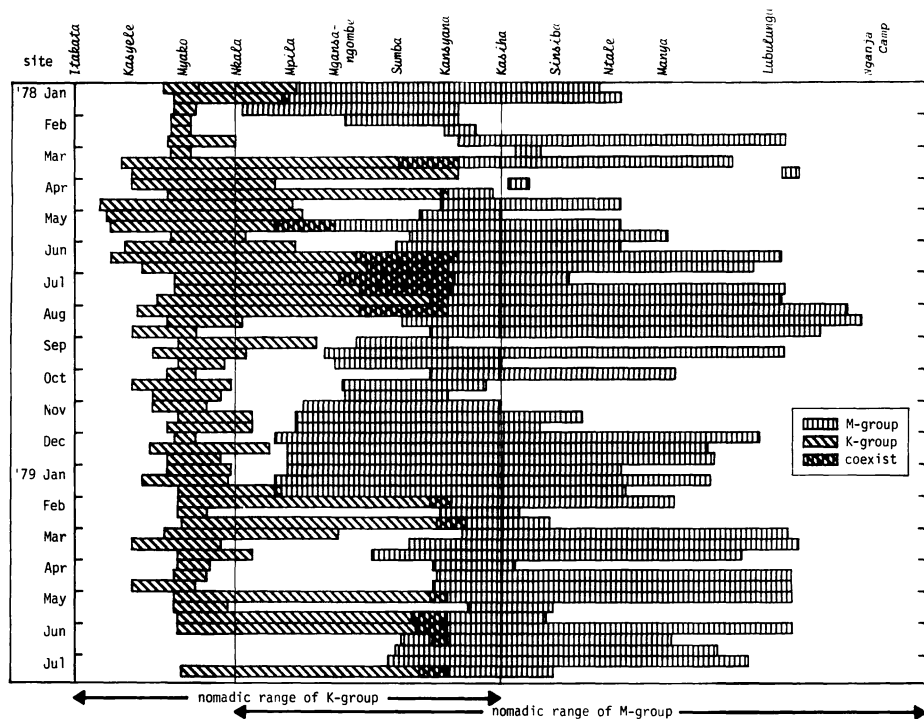


Fig. 7. Spatial relationships between M- and K-groups between January 1978 and July 1979. Each horizontal bar indicates the ten day range of each unit-group. (Source of data is as Fig. 4.)

(Fig. 1), and were seen after January 1974. Therefore, it may not be impossible to consider that inter-unit-group cannibalism in Mahale had some connections with the above mentioned changes in relationships between the two unit-groups. But it is still unclear what kind of effects such changes as the above worked on M-3 and M-4 which were not inter-unit-group cannibalism.

(2) Relationships between M- and K-groups concerning exchange of females

We have paid attention to dyadic relationships between M- and K-groups, on the basis of their spatial relationship and that they frequently exchanged their females (Kawanaka & Nishida, 1975; Nishida, 1979). The problem of the transfer of females between the two unit-groups will be examined again adding the data gained in the subsequent researches. Since females of M-group have not been satisfactorily traced, I will here examine those of the following two categories: (1) 9 females who were born in K-group and grew up to reach the age of sexual maturity therein, and (2) 8 females who (probably) joined K-group from outside (Table 8).

All of the 9 females of category (1) have the experience of leaving K-group at least once. After leaving, 4 of them have never been seen in M-group, even though they were distinctly identified, nor did they return to K-group, so that they were thought to have joined another unit-group or to have died. The remaining 5 have joined M-group and all of them became estrous therein. Thus, more than half of the females who were born in K-group have transferred to M-group. 5 of 8 females of category (2) transferred to M-group after they joined K-group, but the other 3 have remained in K-group ever since they joined it.

Table 8. Number of females who transferred from K- to M-group since 1965.* (Including unpublished data gained by Nishida, Uehara, Norikoshi and Mori.)

	no. of females	have left K-group			
		(total)	have joined M-group	haven't joined M-group	haven't left K-group
born in K-group	9	9	5	4	0
joined** K-group	8	5	5	0	3
total	17	14	10	4	3

*: cases of those who have belonged to K-group ever since 1965 but whose native unit-groups were unknown are omitted.

**: their native unit-groups are unknown.

Although the data gained so far are still insufficient, more than 10 of the 17 females (more than 58.8 %) have belonged to both K- and M-groups, so that it seems to be possible, as pointed out in our previous papers, that these two unit-groups frequently exchange their females with each other. It may be possible to say that in chimpanzee society there exists a dyad of unit-groups between which females frequently transfer, though it cannot be necessarily affirmed that a couple of unit-groups may be organized into, so to speak, two moieties (Itani, 1974).

(3) Birth, infant mortality, and ratio of cannibalism to the whole infant mortality factors in Mahale

More than 45 cases of delivery have been known in Mahale since 1965: of them (i) 1 case was that a female born in K-group had an infant in K-group, (ii) 13 cases were that those who were confirmed to have transferred had infants in unit-groups which they joined, and (iii) 19 cases were that those who have belonged to K-group ever since the beginning of researches but whose native unit-groups were not known had infants in K-group. Although the cases of delivery in M-group other than (ii) have been recorded and infants or juveniles whose birth years were not known were seen in M-group, descents of their mothers were not known and not a few infants seem to have born in this unit-group but have died without being seen by the observers, since this unit-group has not been traced satisfactorily. Therefore, only the 33 cases in total of (i), (ii) and (iii) will be examined here, omitting the cases in M-group except (ii) (Table 9).

The data summed up in Table 9 are not usable for a demographic study, since infants' ages and longevities were disregarded, but a rough trend can be grasped from them. A point that first draws our attention is that mortality rate as a whole was high and particularly that of male infants was considerably high (60.0 %), which was twice as high as that of female infants (36.4 %). Consequently males in July 1979 were nearly equal in number to females (♂ ♂ : ♀ ♀ = 7:5), even though twice as many males as females were born (♂ ♂ : ♀ ♀ = 20:11).

The reason for the high mortality rate of male infants is not known, while it is worth noting that 4 of 12 cases of male mortality (33.3 %) was due to cannibalism. The real ratio of cannibalism to the whole male mortality factors would be smaller, considering that there is no evidence that infants given birth to by females of M-group who do not belong to category (ii), which was not a subject to be examined here, fell victims to cannibalism. Nonetheless this may not be negligible. Thus, males died in the early stages of life at a higher rate than females, due, in part, to cannibalism.

It would also be worth noting that the 4 victims of cannibalism in Mahale were infants

Table 9. Cases of delivery in Mahale since 1965, and life and death of infants.* (Including unpublished data gained by Nishida, Uehara, Norikoshi and Mori.)

	infant's sex	no. of cases	live in July '79	died by July '79 on			whereabouts unknown
				(total)	cannibalism	other factor	
I	♂	1	1	0	0	0	0
	♀	0	0	0	0	0	0
	total	1	1	0	0	0	0
II	♂	8	2	5	4	1	1
	♀	4	3	1	0	1	0
	?	1	0	1	0	1	0
	total	13	5	7	4	3	1
III	♂	11	4	7	0	7	0
	♂	7	2	3	0	3	2
	?	1	0	1	0	1	0
	total	19	6	11	0	11	2
I+II+III	♂	20	7	12	4	8	1
	♀	11	5	4	0	4	2
	?	2	0	2	0	2	0
	sum total	33	12	18	4	14	3

*: cases in M-group which did not fall under II are omitted.

I: cases in which females had infants in their native unit-groups.

II: cases in which females had infants in unit-group which they joined.

III: cases in which females of K-group whose native unit-groups are unknown had infants therein.

which fall under category (ii), that is, those which females conceived in unit-groups which they joined. All the victims of category (b) in Gombe were infants to which their mothers gave birth in their own native unit-group (or very probably so), but such cases have never been seen in Mahale.

6. DISCUSSION

(1) Causation of infanticide from an ecological point of view

Goodall (1977) states that inter-community infanticide recently began to be seen in Gombe and considers that this may have some connections with a rise in population density therein or an increase in chances of encounters between neighboring communities. Also in Mahale, it was in 1974, 10 years after researches were begun in 1965, when the first case of cannibalism was observed, and the possibility could not be denied that inter-unit-group cannibalism had some relations with changes in spatial relationships and with a rise in population density in a limited area.

In langur monkeys in which many cases of infanticide have been reported, the correlation between frequency of the incidents and population density has been pointed out (Sugiyama, 1965, 1980; Mohnot, 1971; Rudran, 1973; Hrdy, 1974; Parthasarathy & Rahaman, 1974), and in crab-eating monkeys the possibility of a similar correlation is suggested as well (Angust & Thommen, 1977). Although this point in gorillas is not examined, there may generally exist this correlation in non-human primates in which infanticide is committed. But it has not yet been made clear in any species whether there were a critical point concerning the occurrence of infanticide in population density.

Goodall (1977, p. 272) also says on infanticide in chimpanzees that "we should, perhaps, consider the killing of stranger infants within overall patterns of aggression between neigh-

boring communities” and that “those attacks which led to killing of stranger infants were aimed as much (or more so) to injuring the *mother* as infant”.

Certainly it is said that, in M-2 of inter-unit-group cannibalism in Mahale, the victim's mother seems to have been attacked severely by the captors (Nishida et al., 1979). It has been well known both in Gombe and in Mahale that males of neighboring unit-groups were antagonistic to each other (Goodall et al., 1979; Goodall, 1979; Nishida, 1979). However, a unit-group is highly tolerant to sexually active females approaching it from the outside. Besides, although Nishida saw several ‘stranger’ females with dependent young mingling with members of K-group in 1966 (Nishida & Kawanaka, 1972; Nishida, 1979), he never saw such a scene in which these females or their offspring were attacked by members of K-group. While attacks on ‘stranger’ females which did not result in infanticide have been found in Gombe (Goodall et al., 1979), the above cases in Mahale may imply that the approach of ‘stranger’ females with dependent young does not always give rise to aggression against them.

In Mahale, along with the above changes in chimpanzees, research formation has been changed recently. In the early stages, researches were made interruptedly and K- and M-groups were rarely traced at the same time (Nishida, 1979). Since 1975, however, both unit-groups have been traced simultaneously throughout the year. It cannot be denied, therefore, that such an infrequent phenomenon as cannibalism was more easily detected because of this change. Also in Gombe such changes occurred that researchers increased in number and new research methods like individual tracing were adopted (e.g. Goodall, 1979). It may not be denied as well that these have some relations with the fact that infanticide and cannibalism have been seen in recent years therein.

Examining the past cases of infant mortality in the Kasakela community, Goodall (1977) says that there is a possibility that some of the infants have fallen victims to infanticide in the past, and considers that all these were the victims of intra-community infanticide. However, since it is unclear whether there is a critical point in population density concerning the occurrence of inter-unit-group infanticide or not, it should be said that there is no firm grounds for considering that inter-unit-group infanticide has never occurred before 1971.

It has been pointed out that infanticide in langurs may have such a function as prohibition of rise in population density to maintain an ecological balance between their population size and their habitat (Sugiyama, 1965, 1980; Rudran, 1973; Hrdy, 1974). In chimpanzees, however, it is still unclear whether their infanticide has some ecological advantage or not.

(2) Sociological significance of infanticide

The sociological significance of infanticide in chimpanzees has been discussed in comparison with that in langurs and that in gorillas by every researchers (Suzuki, 1971; Bygott, 1972; Goodall, 1977; Itani, 1977; Norikoshi, 1978; Nishida et al., 1979). Among them, Nishida et al. (1979, pp. 18–19) say that “cannibalism may be an extension of infanticide, which may function in changing ‘mother’ into ‘female’” and that “it is possible that chimpanzee cannibalism may have some relations to a female transfer system among neighboring unit-groups”; similar points are also suggested by Goodall (1977) and Itani (1977).

If we pay attention to Wakasunga's movements only during the period after her delivery, it might be possible that they agree with the statements by Nishida and others. However, if we took a longer period, e.g. after her conception, her movements could not agree with their statements. As both Goodall (1977) and Nishida et al., (1979) describe, none of the victims' mothers other than Wakasunga have been confirmed as transferring after the incidents. By contrast, not a few of them remained in the same unit-groups as those to which they had belonged before the incidents and had babies again therein.

Infanticide in langurs occurred following usurpation of a one-male troop by lone males and

was committed by a male that newly joined the troop (Sugiyama, 1965, 1980; Mohnot, 1971; Hrdy, 1974; Parthasarathy & Rahaman, 1974), and that in the colony of crab-eating monkeys kept in a cage in the Bazel Zoo was committed by a male who had newly attained the status of alpha male (Angust & Thommen, 1977). Thus, in these species of Cercopithecidae, every case of infanticide occurred within a troop after a social change and was committed by a male alone. It is also said that infanticide in these species has such functions as activating sexuality of females losing infants, so that the male has sexual relations with them to integrate the troop as soon as possible, and as removing the offsprings of his predecessor but producing his own offsprings earlier than otherwise.

The cases of infanticide in gorillas seem to be classified into two: (1) an infant is harmed by a lone male or by a male of a neighboring group, and (2) it is harmed by females of its own group. It is said that, in some of the former cases, the lone male is likely to kidnap the female losing an infant to form a new group (Fossey, 1979; Harcourt, 1979).

It is possible, therefore, that infanticide in chimpanzees and in gorillas shares such common features as that both sexes harm infants, that the incidents do not always occur within a social unit, and that they are not preceded by social changes. So it should be said that the incidents in these two species of Pongidae occur in clearly different social context from those in Cercopithecidae. But, even between chimpanzees and gorillas, such differences can be noted as that the cases in gorillas in which a male harmed an infant are (likely to be) followed by a social change, while in chimpanzees at least the formation of a new group cannot occur, and that a male gorilla belonging to a group has never been seen to kill an infant of his own group.

Then, what is the sociological significance of infanticide in chimpanzees which occurs in clearly different context from Cercopithecidae and partly different from gorillas? I would like to discuss two points to which little attention has been paid so far. The first is its connection with incest. Chimpanzee males are quite stable as members of a unit-group, while almost all females who grow up to reach the age of sexual maturity leave their native unit-groups and join other ones (Kawanaka & Nishida, 1975; Nishida, 1979; Pusey, 1979). It has been already pointed out that this 'stability of males and transfer of females' works as a mechanism for avoidance of incest between a father and a daughter, and between siblings, that is to say, between relatives of the first to second degree (Itani, 1972a, b, 1976; Nishida, 1979; Pusey, 1979).

M- and K-groups in Mahale have exchanged many females between them, though all of their females did not transfer only between these two unit-groups, so that it is possible that these two have what can be called dyadic structure. Although it is not yet made clear whether such inter-unit-group relationships generally exist in chimpanzee society or not, if this is the case, the following may be possible.

If a female A born in X-group transfers to Y-group and has female offspring B therein, it will be highly probable that, after attaining the age of sexual maturity, B will transfer to X-group where her mother A was born. If B will do this and give birth to a child C in X-group, it may be possible that C is born in consequence of sexual intercourse between B and her relatives of the second to fourth degree, because it is very probable that in X-group there are A's father, brothers and nephews (that is, B's grandfather, uncles and cousins on her mother's line).

In other words, although 'stability of males and transfer of females' can serve for avoidance of incest between relatives of the first to second degree, if particular two unit-groups have dyadic structure in chimpanzee society, it should be considered that relatives of the second to fourth degree are rather likely to commit incest between them. Here is no room for psychological resistance derived from acquaintance between individuals to work. However, infanticide may result in removing infants born in consequence of incest.

The victim's mother of M-3, Ndilo was born in K-group but the native unit-group of her mother (that is, grandmother of the victim) is not known. If this was born in M-group, it seems to be possible that this case agrees with the above speculation.

All the 4 victims of intra-community infanticide in Gombe were infants whom their mothers conceived in their own native community. It seems to be not impossible that these infants were born in consequence of incest between nearer relatives than the above case. If so, infanticide might result in removing those produced by relatives of the first to second degree.

It is suggested that infanticide in langurs and in gorillas may play a role of removing infants produced through incest between a father and his daughters (Itani, 1972b, 1977). In this point, infanticide in chimpanzees might have a similar function. Being considered in this way, although it is not yet clear at all how the captors are driven into committing infanticide, it can be said that all the cases have the same effect irrespective of whether they occur within a unit-group or between them, or of whether the captors are males or female. It was because of this speculation that I clung to the examination of personal histories of the victims' mothers.

However, chimpanzee females do not always confine themselves to belonging to particular two unit-groups throughout their lifetime. Besides, not a few offspring grew up in safety irrespective of whether they were born in their mothers' native unit-groups or in those which their mothers joined. Supposing that there may be some connection between infanticide and the removal of infants produced through incest, we can gain one way for approaching this problem without regard to the captor's motivation. This demands, however, that life histories of females must be known at least up to the second ascending generation from the infant in question, which requires future, continuous researches.

Another problem is whether infanticide has some connection with the composition of a unit-group. Since the existence of a unit-group in chimpanzees has been confirmed, it has been said to be a question why males are fewer than females and why young adult males are particularly few, though this did not fit for all unit-groups (Itani & Suzuki, 1967; Itani, 1972a, 1974; Nishida, 1968, 1979).

In Japanese monkeys, in which a troop continues in a female line and males leave their own native troop, males are always fewer than females in a troop, though sex ratio of newborns is nearly equal between both sexes (Kawai, 1964). This is not unrelated with that there are males leading a solitary life without belonging to a troop (e.g. Nishida, 1966). On the other hand, in chimpanzees, females who transfer between unit-groups are more in number than males within a unit-group. It may be said that this is partly caused by the facts that, after leaving a unit-group, a female seems to join a neighboring one without leading a solitary life (Nishida & Kawanaka, 1972), and that, although cases of males leaving a unit-group have been known, those in which fully grown males join a unit-group have never been recorded (Kawanaka & Nishida, 1975; Nishida, 1979; Pusey, 1979).

Recently, some cases of intra-specific killing have been reported from Gombe that several males who left the community when it divided into two were so badly injured by those of the original community that they died (Goodall et al., 1979; Goodall, 1979). Also in Mahale, several males left K-group since 1974, which was supposed to be a phenomenon appearing in a similar context to the above incidents (Nishida, personal communication; Itani, 1977).

This seems, however, to be still insufficient to explain the small number of males, especially of young adult males in a unit-group. Then, it should be noted that male infants were harmed by conspecifics more in number than female ones. If there is no way for recruiting males to a unit-group except for delivery, loss of male infants by infanticide should bring about a disproportionate sex ratio in a unit-group, even though the frequency of infanticide is not high in any way.

Although the foregoing arguments were put forward on the basis of results, it may be said

these show that infanticide in chimpanzees should not be considered apart from their social structure. But both of them are satisfied only by 'killing' infants. Reasons for and the significance of 'eating' them should be looked for elsewhere.

(3) Motivation for infanticide and for cannibalism

Males and females of chimpanzees seem to be driven into killing infants of conspecifics in different ways. In gorillas in which both sexes also commit infanticide, social context in which the incidents occur and their social significance seem to be different according to the captor's sex. Besides, a male gorilla was never seen to eat the carcass, though it was thought that females ate a carcass. These may imply that both sexes of gorilla are not driven by the same motives as those of chimpanzees; it may be said that these two species also share a common feature in this respect.

Both in langurs and crab-eating monkeys, only males harm infants of conspecifics and it is suggested that they are driven by 'sexual desire' (Sugiyama, 1965, 1980) or "an increased level of plasma-testosterone concentration, induced by a sudden 'outbreak' of high sexual activity and the assertion of dominance as alpha male" (Angust & Thommen, 1977, p. 222). In chimpanzees, however, at least the captor in M-4 cannot be thought to be driven into killing an infant by 'sexual desire'. This may be another point in which chimpanzee and Cercopithecidae are different from each other.

Among the 12 cases of infanticide in chimpanzees dealt with in this paper, there were cases where the captors continuously and almost entirely consumed the carcasses (G-2, -6, -7, M-4), while some of the others were where they killed infants but did not eat the carcasses (G-4, -5). Besides, in Gombe, adults were seen to fall victims to intra-specific killing, but they were not eaten (Goodall et al., 1979; Goodall, 1979).

It should be considered, therefore, that motivations for cannibalism consist of two elements: that for 'killing' conspecific, and another for 'eating' its carcass. When classifying the cases in Gombe into two categories, Goodall (1977) seems to adopt, as an important criterion, the point whether the captors eat the carcass or not. However, it cannot yet be made clear by the data gained so far how chimpanzees choose between eating the carcass and not; the data are still insufficient for ethological analysis.

Paying attention to that "cannibalism conspicuously increases in higher primates", Itani (1977, pp. 237-238) considers that "this may not be a phenomenon showing their primitiveness such as aggression but that appearing because they have highly evolved or because they have been half untied from instinct". Certainly, among non-human primates, infanticide is not a universal phenomenon, though it is said that infanticide has been found in 8 genera of *Presbytis*, *Pygathrix*, *Theropithecus*, *Papio*, *Macaca*, *Cercopithecus*, *Pan*, and *Gorilla* (Angust & Thommen, 1977). Much fewer eat the carcass; in addition to cases in chimpanzees and in gorillas, only one case has been seen in *Papio ursinus* (Saayman, 1971) and two cases in *Cercopithecus ascanius* (Strusaker, 1978) in natural conditions.

In contrast, within Hominidae, intra-specific killing and cannibalism occur quite universally, and many evidences of them have been found in their fossil remains (Roper, 1969). It may not be impossible to consider, therefore, that infanticide and cannibalism in chimpanzees and in gorillas share the common roots with those in Hominidae (Suzuki, 1971; Goodall, 1977). Accumulation and more detailed examination of the data of this problem will offer an important clue for understanding the process of hominization.

7. SUMMARY

A new case of cannibalism was observed among chimpanzees in the Mahale Mountains in

June 1979. The victim was a 1.5-month-old male infant to whom his mother gave birth after she had transferred from K- to M-group and had been copulated with by males of M-group. The captor was a male of M-group, who almost entirely consumed the carcass within 3 hours, together with some other males and one female.

The cases of infanticide and cannibalism reported so far and our case, 12 in total, were compared with each other and such points as the following were found: (1) more male infants were killed by conspecifics than female ones, (2) relations between the victims' mothers and the captors were more complicated than had been thought, and could not be so simply categorized, (3) the captors did not always kill offspring begeted by males of unit-groups other than their own, and (4) it seems to be possible that infanticide and cannibalism had connection with changes in inter-unit-group relationships.

The following were found by examining the data from Mahale: (1) sexual desire could not be thought to be direct motivation for infanticide even in the cases where males were the captors, (2) particular two unit-groups tended to frequently exchange females with each other and there was a possibility that incest between relatives in the second to fourth degree was committed, and (3) the mortality rate of male infants was much higher than that of female ones, and the ratio of the loss caused by cannibalism to the whole male infant mortality factors could not be disregarded. It may be thought, therefore, that infanticide and cannibalism in chimpanzees may result in removal of offspring born out of incest, and may be one cause which brings an unbalanced sex ratio to a unit-group. This, then, implies that they should not be considered apart from their social structure.

Infanticide and cannibalism in chimpanzees must be phenomena closely related with those in gorillas, despite some differences between them. They occurred in a different social context from infanticide observed in *Cercopithecidae* like langurs and crab-eating monkeys, but it may be not impossible to consider that they share common roots with those in *Hominidae*.

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